

Comparative Larval Development of *Peprilus burti*, *P. triacanthus* and *P. paru* (Pisces: Stromateidae) from the Western North Atlantic

JAMES G. DITTY AND FRANK M. TRUESDALE

Melanophores formed diagnostic lateral bands, one above and one below the midline on *P. paru* less than about 5.5 mm SL; only the lateral surface of the caudal peduncle and the immediately adjacent portion of the trunk remained sparsely pigmented. Conversely, *P. burti* and *P. triacanthus* less than about 5.5 mm SL had 1-2 lateral melanophores. *P. paru* was significantly deeper-bodied than *P. triacanthus* by 7.5 mm SL and *P. burti* by 9.5 mm SL. *P. burti* and *P. triacanthus* less than 4 mm SL were usually separable by the number of ventral midline melanophores. *P. burti* usually (92%; N = 50) had 4-8 melanophores between the hindgut and notochord tip, whereas most (94%; N = 50) *P. triacanthus* had 11-17. Above 4 mm SL, *P. triacanthus* was usually more densely pigmented than *P. burti* of comparable size. Differences in morphometrics were not sufficiently distinct to reliably separate *P. burti* and *P. triacanthus*. *P. paru* consistently had 17 caudal vertebrae, whereas *P. burti* and *P. triacanthus* had 17-18 and 18-19, respectively. However, on specimens greater than 7 mm SL, 86% (N = 22) of *P. burti* had 17 caudal vertebrae, whereas 79% (N = 19) of *P. triacanthus* had 19. Developmental morphology does little to augment our understanding of the relationship between *P. burti* and *P. triacanthus*. Although larvae of both are extremely similar, subtle differences in pigmentation and modally different vertebral counts allow most specimens to be assigned to recognizable types.

THREE species of *Peprilus* occur in the western North Atlantic: the Gulf butterfish, *P. burti* Fowler; the Atlantic butterfish, *P. triacanthus* (Peck); and the harvestfish, *P. paru* (Linnaeus) (Horn, 1970). Robins et al. (1980) listed *P. alepidotus* as the harvestfish of US coastal waters but I follow Horn (1970) in considering

P. alepidotus as a junior synonym of *P. paru*. *P. triacanthus* and *P. burti* are geminate species whose present taxonomic status is based primarily on caudal vertebrae number (Horn, 1970; Perschbacher et al., 1979). *P. burti* occurs in the northern Gulf of Mexico and *P. triacanthus* along the Atlantic coast of the U.S.; both species are

absent from southernmost Florida (Horn, 1970). Recently, Perschbacher et al. (1979) reported incursions of large numbers of *P. burti* during 1977 into the Atlantic, mostly off North Carolina but with one occurrence in Virginia. The range of *P. paru* includes the Atlantic coast of the U.S. as well as the Gulf of Mexico with a continuous distribution around Florida (Horn, 1970).

Little is known of *Peprilus* larvae although the adults are usually common and of some commercial importance. Only the larvae and early juveniles of *P. simillimus* (Pacific pompano) have been described in detail (D'Vincent et al., 1980); precise morphometric, meristic and pigmentation data are lacking for larvae of western North Atlantic species. Pearson (1941) briefly described larvae and juveniles of *P. paru*. Colton and Honey (1963) described eggs and early larvae and Lippson and Moran (1974) described larvae and a juvenile, of *P. triacanthus*. These and other observations on the early life history stages of *P. triacanthus* and *P. paru* have been summarized by Martin and Drewry (1978). The larvae of *P. burti* have not been previously described.

MATERIALS AND METHODS

Peprilus larvae were obtained from plankton collections taken in three major areas: Mid-Atlantic Bight (New Jersey to Virginia), South Atlantic Bight (North Carolina to Florida) and the Gulf of Mexico. Sources of material are detailed in Ditty (1981).

Larvae of *P. paru* were separated from those of *P. burti* and *P. triacanthus* by using characters from Pearson (1941). Initial screening of larvae for *P. burti* and *P. triacanthus* was based on distributional information of the adults (Caldwell, 1961; Horn, 1970; Perschbacher et al., 1979). Those *Peprilus* larvae (non-*P. paru*) from north of Cape Hatteras and those from the Gulf of Mexico were considered probable *P. triacanthus* and *P. burti* respectively and were examined for morphological and pigmentation differences. We determined that indeed two larval types existed and that a developmental series of the larvae from north of Cape Hatteras was linked through meristics to unequivocal *P. triacanthus* juveniles and that from the Gulf to *P. burti*.

All *Peprilus* larvae ($N = 399$) had been in 3–5% buffered formalin except for three specimens in alcohol. Body measurements were made to the nearest 0.01 mm with an ocular microm-

eter in a dissecting scope and were defined as follows:

Standard length (SL)—snout tip to notochord tip; or when caudal fin is formed, from tip of snout to posterior margin of hypural bones. Snout length—snout tip to anterior margin of orbit.

Eye diameter—anterior to posterior margin of pigmented portion of eye.

Head length—snout tip to posterior margin of cleithrum.

Preanal length—snout tip to vertical line through posterior margin of anus.

Depth at pectoral fin base—depth measured perpendicular to longitudinal body axis at anterior margin of pectoral base.

Depth at anus—depth measured perpendicular to longitudinal body axis at posterior margin of anus.

Representative specimens of each species were illustrated with the aid of a camera lucida. Differential staining of larvae (Dingerkus and Uhler, 1977; Fritzsche and Johnson, 1980) allowed discrimination of cartilage and bone; initial uptake of Alizarin Red was considered the onset of ossification. Spines were enumerated when they resembled formed structures, rays when initially segmented. Terminology of caudal elements follows Gosline (1960, 1961). The larval period was separated into three developmental stages: preflexion, flexion and postflexion (Ahlgren et al., 1976). Transition larvae were distinguished from early juveniles by the attainment in the latter of both a full complement of rays in all fins and initial development of scales.

Regression analyses were used to define the relationship between standard length and each body measurement. Regression lines were compared among the species according to Neter and Wasserman (1974).

RESULTS

Morphological development.—Smallest larvae of all three species had large, blunt heads and irregularly circular eyes. In each, the body was deepest near the pectoral fin and tapered abruptly behind the anus. The gas bladder, conspicuous above the visceral mass, slowly became obscured by overlying musculature and pigment as development progressed. The visceral mass was prominent and a single intestinal loop was visible through the body wall. The yolk-sac

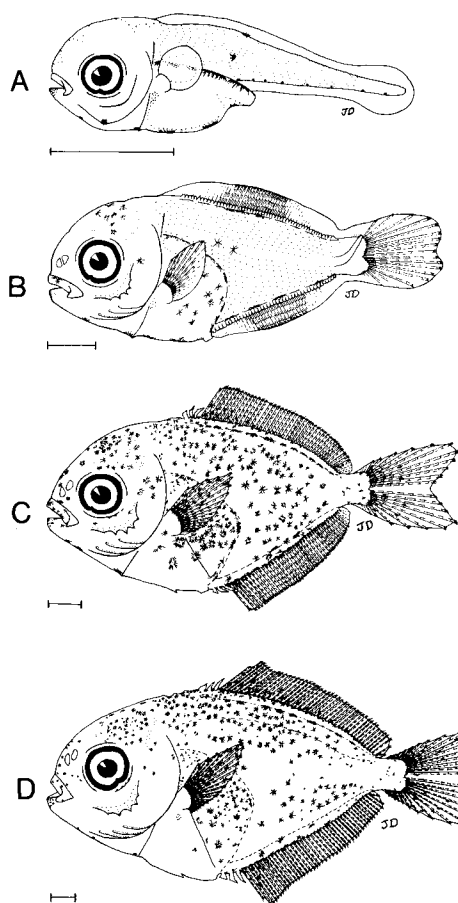


Fig. 1. Development of *Peprilus burti*. A) 2.88 mm SL. B) 6.55 mm SL. C) 9.90 mm SL. D) 14.85 mm SL. Solid lines represent 1 mm.

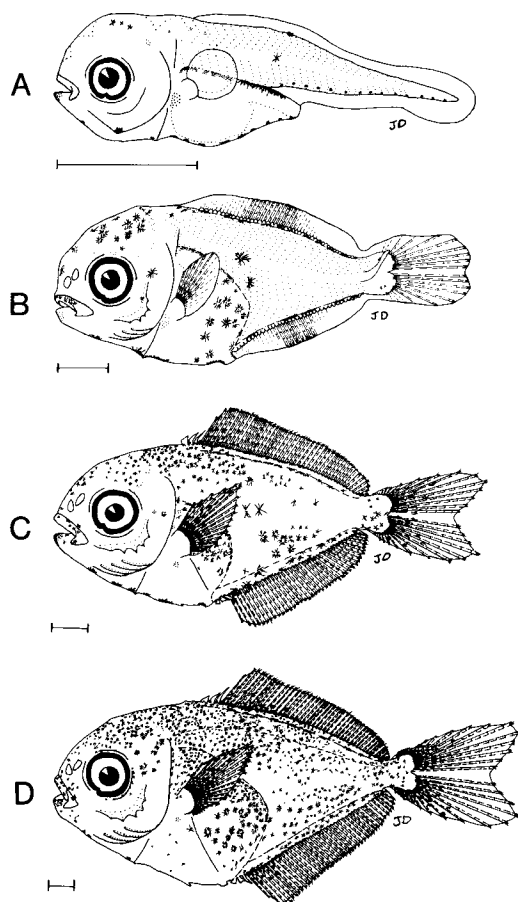


Fig. 2. Development of *Peprilus triacanthus*. A) 3.00 mm SL. B) 6.55 mm SL. C) 9.80 mm SL. D) 14.70 mm SL. Solid lines represent 1 mm.

was absent. The hindgut and anus projected posteriad to near midbody but gradually shifted antero-ventrad as larvae developed (Figs. 1, 2, 3). This shift was reflected in a proportionate decrease in preanal length (Table 1).

The linear statistical model was appropriate in all cases to describe the relationship between each morphometric and standard length; the statistics for all regression lines were given in Ditty (1981). Differences in eye diameter, snout, head and preanal lengths between the three species were not diagnostic. Comparisons among species of regression lines for each of these morphometrics on standard length showed overlap of confidence limits ($P < 0.05$) for predicted values. Depth at pectoral and depth at anus measurements were of some diagnostic value.

P. paru was deeper-bodied (no overlap of 95% confidence limits on predicted values of depths at pectoral and at anus) than *P. triacanthus* and *P. burti* by 7.5 mm SL and 9.5 mm SL, respectively. Differences in depth between *P. burti* and *P. triacanthus* were not diagnostic; although by early juvenile stage *P. burti* was slightly more convex in profile than *P. triacanthus* (Figs. 1D, 2D, Table 2).

Pigmentation of P. burti and P. triacanthus.—All larvae examined had pigmented eyes. Pigment was also present on the tip of the mandible at all sizes. By 3–4 mm SL, external pigment was present near both the dorsal articulation of the preopercle and opercle and on the tip of the

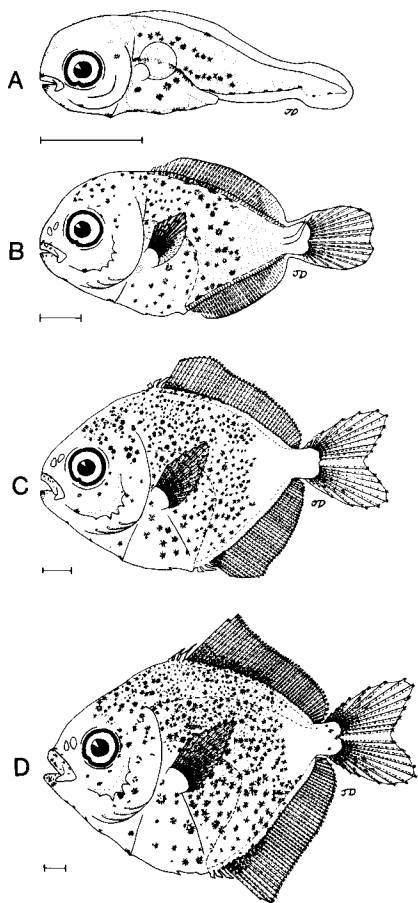


Fig. 3. Development of *Peprilus paru*. A) 2.88 mm SL. B) 6.55 mm SL. C) 9.82 mm SL. D) 14.80 mm SL. Solid lines represent 1 mm.

premaxillary or snout. Melanophores were present in the nape musculature and scattered both internally and externally over the mid- and hindbrain regions by 4 mm SL on *P. triacanthus*; however, *P. burti* usually lacked this pigmentation until 5–6 mm SL (Figs. 1A, B, 2A, B). One or two diffuse, external melanophores were usually visible over the forebrain by 5–6 mm SL on *P. triacanthus* and about 7–8 mm SL on *P. burti* (Figs. 1C, 2B). On both species, melanophores were added over the head region throughout the developmental period.

Larvae of both species at all sizes had melanophores on the anterolateral visceral mass adjacent to the pectoral base, distributed over the posterior visceral mass and along the dorsal wall of the gas bladder. By 3 mm SL, single, external

melanophores were present along both the lateral and dorsal midlines near midbody. As the dorsal fin began to differentiate (approximately 4 mm SL), the dorsal melanophore on the midline became embedded in the musculature along the fin base. Pigmentation increased along the dorsal base as development progressed. Larvae were sparsely pigmented laterally until approximately 7–8 mm SL when melanophores were added along the trunk (Figs. 1A–C, 2A–C). As juvenile stage approached, trunk pigmentation intensified (Figs. 1D, 2D).

Along the ventral midline, a series of external melanophores traversed the visceral mass, and posteriad, a series of internal and external, punctate melanophores extended between the hindgut and notochord tip (Figs. 1A, 2A). Ninety-two percent ($N = 50$) of *P. burti* less than 4 mm SL had 4–8 melanophores between the hindgut and notochord tip, whereas 94% ($N = 50$) of *P. triacanthus* had 11–17. These melanophores posterior to the hindgut frequently began to expand and radiate into the interhaemal musculature by 5 mm SL on both species.

Internal melanophores were present over the pericardium by 3–4 mm SL but were usually obscured by the operculum and gill arches. On larvae greater than 3.5–4 mm SL, pigment was present immediately dorsal and ventral to the anterior notochord and as development continued, this pigment extended posteriad and radiated distally along the neural and haemal spines. On larvae 8–10 mm SL, all internal pigment was obscured by overlying musculature and integument.

Melanophores first appeared on the pectoral and dorsal fin rays of specimens about 8 mm SL and on the anal fin rays of those about 10 mm SL (Figs. 1C, D, 2C, D). Sometimes a small, punctate melanophore was evident on the dorsal finfold near the notochord tip on larvae less than 3 mm SL. By approximately 5 mm SL, pigment outlined the lobes of the caudal fin, and extended onto the principal rays as development progressed (Figs. 1B–D, 2B–D).

Pigmentation of *P. paru*.—All larvae examined had pigmented eyes. Pigment was also present on the tip of the mandible at all sizes. In addition, a series of internal and external melanophores along the mid- and hindbrain regions formed a scattered band which extended toward the eye (Fig. 3A). By approximately 3.5 mm SL, one or two external melanophores were present near both the premaxillary symphysis

TABLE 1. BODY PROPORTIONS (MEAN, STANDARD DEVIATION, AND RANGE) OF LARVAE AND EARLY JUVENILES OF *Peprilus burti*, *P. triacanthus* AND *P. paru*, EXPRESSED AS % STANDARD LENGTH (SL).

Species and stage	Size range (mm SL)	N	Snout length	Eye diameter	Head length	Preal anal length	Depth at pectoral	Depth at anus
<i>P. burti</i>								
Preflexion	2.16–4.64	35	6.8 ± 1.3 (4.1–9.1)	12.3 ± 1.4 (8.6–15.6)	32.2 ± 3.1 (26.3–39.1)	58.5 ± 3.6 (51.6–67.5)	32.7 ± 4.8 (24.1–45.3)	16.8 ± 4.5 (10.5–28.2)
Flexion	3.72–5.47	12	7.8 ± 1.1 (6.4–9.7)	11.6 ± 1.3 (10.0–13.9)	31.2 ± 3.1 (23.9–36.0)	55.0 ± 2.5 (50.6–58.5)	34.6 ± 3.9 (29.6–41.2)	22.0 ± 4.1 (15.8–29.2)
Postflexion	4.92– 13.86	89	9.4 ± 1.3 (5.5–12.9)	13.5 ± 1.1 (10.8–16.8)	36.4 ± 2.7 (30.7–45.9)	52.6 ± 3.3 (43.5–60.7)	48.3 ± 6.4 (35.0–56.7)	44.4 ± 9.9 (23.5–57.0)
Juvenile	14.08– 19.82	24	9.6 ± 1.2 (7.9–12.0)	12.5 ± 0.9 (10.4–14.2)	35.9 ± 2.2 (31.7–39.6)	49.5 ± 2.3 (45.5–54.2)	55.7 ± 1.4 (53.0–57.9)	56.1 ± 1.1 (53.6–57.9)
<i>P. triacanthus</i>								
Preflexion	2.04–4.11	31	6.8 ± 1.6 (4.1–11.4)	11.1 ± 1.1 (7.5–13.1)	30.5 ± 2.0 (26.9–35.7)	56.0 ± 2.7 (52.0–63.9)	29.6 ± 3.7 (23.5–36.4)	15.5 ± 4.3 (9.2–26.5)
Flexion	3.84–4.76	7	8.0 ± 1.2 (6.7–10.1)	11.9 ± 1.3 (10.0–13.7)	32.3 ± 2.1 (29.4–36.3)	53.4 ± 3.4 (48.4–59.0)	34.6 ± 2.3 (30.6–37.1)	23.2 ± 3.1 (19.4–28.8)
Postflexion	4.46– 13.98	94	8.5 ± 1.0 (6.6–10.6)	13.2 ± 1.1 (10.5–15.8)	35.3 ± 2.1 (29.6–39.6)	50.7 ± 3.7 (43.7–64.4)	45.3 ± 4.7 (32.6–53.1)	40.7 ± 8.4 (23.5–53.1)
Juvenile	14.16– 20.86	27	8.8 ± 0.8 (7.3–10.0)	12.8 ± 0.8 (11.4–14.4)	35.3 ± 1.9 (30.8–37.5)	46.6 ± 2.0 (43.1–51.9)	52.1 ± 1.8 (48.1–54.6)	52.3 ± 1.8 (48.1–55.3)
<i>P. paru</i>								
Preflexion	1.85–3.48	21	6.4 ± 1.5 (3.4–9.2)	11.5 ± 1.4 (9.1–14.3)	31.9 ± 4.2 (21.6–38.7)	58.8 ± 3.1 (51.9–65.5)	29.7 ± 5.2 (20.5–40.8)	14.0 ± 4.0 (7.6–22.2)
Flexion	3.48–4.25	5	7.8 ± 0.6 (6.9–8.6)	12.5 ± 0.6 (11.8–13.3)	36.8 ± 4.0 (31.5–41.5)	58.6 ± 3.5 (54.8–63.3)	39.5 ± 3.9 (35.1–43.9)	23.1 ± 4.1 (20.1–30.0)
Postflexion	4.44– 10.89	29	9.4 ± 1.0 (7.6–11.2)	14.8 ± 1.2 (11.3–16.5)	40.5 ± 2.8 (35.7–46.1)	52.8 ± 3.4 (46.9–59.5)	61.4 ± 7.6 (47.0–71.8)	59.6 ± 9.8 (36.4–71.0)
Juvenile	11.01– 18.92	25	9.9 ± 1.1 (7.5–11.8)	14.1 ± 0.8 (12.2–15.4)	40.0 ± 2.3 (35.0–44.6)	51.4 ± 4.3 (43.2–58.6)	69.5 ± 3.2 (63.3–75.0)	69.5 ± 3.0 (63.3–74.7)

and dorsal articulation of the preopercular and opercular bones (Fig. 3B). Pigmentation of the head region increased with standard length.

A patch of pigment was present on the anterolateral visceral mass adjacent to the pectoral base. Melanophores were also distributed along the dorsal wall of the gas bladder and over the posterior visceral mass at all sizes. Laterally, external stellate melanophores formed a band, one dorsal and one ventral to the midline, by 2 mm SL. By 3 mm SL, the ventral band traversed the visceral mass, ending below the pectoral base (Fig. 3A). Pigmentation increased and these bands became indistinct, and by approximately 5.5 mm SL, only the lateral surface of the caudal peduncle and immediately adjacent portion of the trunk remained sparsely pigmented (Fig. 3A–D).

On larvae less than 3.5 mm SL, an external melanophore was sometimes present near mid-body along the dorsal midline. Along the ventral midline, a series of internal melanophores extended between the cleithral symphysis and notochord tip (Fig. 3A). As the dorsal and anal fin bases began to differentiate (approximately 3.5 mm SL), dorsal and ventral midline pigment became embedded along the base of the respective fins. Pigmentation increased along the dorsal and anal fin bases as larvae increased in standard length.

Internal melanophores were scattered over the pericardium by 3–4 mm SL but were usually obscured by the operculum and gill arches. Pigment was also present above the anterior notochord by 3.5 mm SL, and extended posteriad along the vertebral column as larvae developed.

TABLE 2. STATISTICS DESCRIBING REGRESSION OF DEPTH AT PECTORAL AND DEPTH AT ANUS ON STANDARD LENGTH FOR *Peprilus burti*, *P. triacanthus* AND *P. paru* LARVAE AND EARLY JUVENILES. Standard length in mm.

Body measurement (Y)	Standard length (X)	N	\bar{x}	\bar{y}	Regression equation	R ²
<i>P. burti</i>						
Depth at pectoral	2.16–19.82	160	8.41	4.16	$Y = -1.104 + 0.626X$	0.990
Depth at anus	2.16–19.82	160	8.41	3.86	$Y = -1.822 + 0.676X$	0.987
<i>P. triacanthus</i>						
Depth at pectoral	2.04–20.86	159	8.58	4.03	$Y = -0.861 + 0.570X$	0.995
Depth at anus	2.04–20.86	159	8.58	3.77	$Y = -1.482 + 0.612X$	0.994
<i>P. paru</i>						
Depth at pectoral	1.85–18.92	80	8.36	5.26	$Y = -1.359 + 0.792X$	0.992
Depth at anus	1.85–18.92	80	8.36	5.07	$Y = -1.893 + 0.833X$	0.992

Internal pigmentation was obscured by overlying musculature by 8–10 mm SL.

Pigment was initially dispersed over the upper pectoral rays at 5.5–6 mm SL and extended onto the anteriormost dorsal and anal rays at approximately 8–9 mm SL (Fig. 3B–D). One or two melanophores were present along the posterior margin of the developing upper and lower hypural bones by 4 mm SL. Pigment extended onto the principal caudal rays as development progressed (Fig. 3).

Fin development.—The earliest larvae of each species had pectoral fin buds consisting of a fleshy base and distal rayless blade. A continuous median finfold surrounded the caudal body. As larvae developed, anlagen and eventually lepidotrichia replaced the finfold until only remnants remained along the caudal peduncle. The development of principal caudal rays preceded the simultaneous appearance of rays in the pectoral, dorsal, and anal fins; anterior procurrent caudal rays were the last to form (Table 3).

At 3–3.5 mm SL, a ventral thickening occurred near the tip of the unflexed notochord. When larvae reached initial flexion (3.5–4 mm SL all three species) anlagen began to differentiate obliquely downward in the caudal finfold. As the hypural complex shifted to a terminal position, development proceeded dorsally and ventrally. The adult complement of 17 principal caudal rays was present on most specimens of all three species by 7.1 mm SL. The adult complement of procurrent caudal rays, 6 + 5–6 for *P. paru* and 7–9 + 7–8 for *P. triacanthus* (Miller and Jorgenson, 1973) was attained

on 11 mm SL *P. paru* and 12 mm SL *P. triacanthus*, respectively. Although the adult complement has not been determined for *P. burti*, the largest cleared and stained specimen we examined (14.55 mm SL) had 8 + 7 procurrent caudal rays. This complement was also attained on a 13.5 mm SL specimen. The caudal fin assumed a bilobed shape at approximately 9–10 mm SL on each species.

Development of dorsal and anal fin bases coincided with initial notochord flexion on each species. Fin bases originated as thickened ridges along the anterior dorsal and ventral midlines, respectively, and progressed posteriad; differentiation was complete by 6.5 mm SL on each species. Dorsal and anal anlagen began to form centrally and progressed outward until the full complement of rays was reached in both fins on 8 mm SL *P. paru* and 9 mm SL *P. burti* and *P. triacanthus*.

The dorsal fin of all three species contained 3 or 4 spines. The fourth spine was difficult to distinguish from the anteriormost soft-ray because the former was last to develop and the latter was indistinctly segmented. The anterior rays of the dorsal and anal fins were slightly longer than the posterior rays and these fins assumed a falcate shape on early juveniles of each species.

Upper pectoral rays were initially segmented on all three species about 6.5 mm SL with rays added progressively ventrad; lower rays were much shorter than upper rays. Most specimens of 11 mm SL exhibited the adult complement of rays (17–24, *P. paru*; 17–22, *P. triacanthus*; and 19–23, *P. burti*) (Horn, 1970). *Peprilus* species lack pelvic fins, but a pelvic spine, lo-

TABLE 3. MERISTICS OF CLEARED AND STAINED LARVAL AND EARLY JUVENILE *Peprilus burti*, *P. triacanthus* AND *P. paru*. U₁, Upper Principal; L₂, Lower Secondary; etc. P, Pelvic Spine Present.

Standard length (mm)	N	Caudal fin				Dorsal fin		Anal fin		Pectoral fin	Pelvic spine	Vertebrae	
		U ₂	U ₁	L ₁	L ₂	Spines	Rays	Spines	Rays			Pre- caudal	Caudal
<i>P. burti</i>													
2.64	3	—	—	—	—	—	—	—	—	—	—	—	—
3.60	3	—	—	—	—	—	—	—	—	—	—	—	—
4.52–4.70	3	—	—	—	—	—	—	—	—	—	—	3–8	—
5.30–5.36	3	—	6–7	4–7	—	—	—	—	—	—	—	13	8–10
6.49–6.55	3	—	6–9	5–8	—	0–II	0–20	—	0–31	4–10	—	13	10–17
7.14	3	0–1	8–9	8	1	II–III	21–28	0–I	21–28	10–11	P	13	17
8.33–8.39	3	1–3	9	8	1–3	III–IV	34–39	II–III	35–37	14–16	P	13	17
9.40–9.58	3	2–4	9	8	3–4	IV	42–44	III	38–43	15–16	P	13	17
10.23–10.29	3	4–5	9	8	4–5	III–IV	43–44	III	39–41	17–18	P	13	17–18
11.31–11.42	3	5–6	9	8	5	III–IV	44–45	III	40–42	20–22	P	13	17–18
12.37	3	6	9	8	6	III–IV	43–44	III	40–42	20–22	P	13	17
13.41–13.56	3	7–8	9	8	6–7	IV	43–44	III	40–43	21–22	P	13	17–18
14.45*	1	8	9	8	7	III	44	III	44	23	P	13	17
<i>P. triacanthus</i>													
2.64	3	—	—	—	—	—	—	—	—	—	—	—	—
3.36–3.43	3	—	—	—	—	—	—	—	—	—	—	—	—
4.70–4.76	3	—	—	—	—	—	—	—	—	—	—	—	—
5.36–5.40	3	—	5–7	5–6	—	—	—	—	—	—	—	13	6–10
6.54–6.66	3	—	8	7	—	—	11–15	—	8–14	6–8	—	13	7–19
7.14–7.44	2	0–1	9	8	1	II	23–39	0–II	18–34	8–11	—	13	19
8.33–8.39	2	2	9	8	2–3	III	32–43	I–III	32–39	11–15	P	13	18–19
9.34–9.52	3	4–6	9	8	4–6	III	43–46	III	38–42	15–18	P	13	19
10.12–10.35	3	6	9	8	6	III	45–46	III	38–41	17–18	P	13	18–19
11.60	3	7–8	9	8	6–7	III–IV	45–46	III	39–43	19–20	P	13	19
11.90–12.08	3	7–8	9	8	7	III	44–45	III	40–42	20–21	P	13	18–19
13.22–13.39	2	7–8	9	8	7	III	44–46	III	41–42	21–22	P	13	19
14.75*	1	8	9	8	8	III	44	III	42	21	P	13	18
<i>P. paru</i>													
2.14	1	—	—	—	—	—	—	—	—	—	—	—	—
3.19	1	—	—	—	—	—	—	—	—	—	—	—	—
4.20	1	—	—	—	—	—	—	—	—	—	—	—	—
5.20	1	—	7	7	—	—	—	—	—	—	—	13	11
6.66	1	—	9	8	—	III	29	II	27	14	P	13	17
7.74	1	1	9	8	1	IV	41	III	40	16	P	13	17
8.57	1	2	9	8	1	III	41	III	38	19	P	13	17
9.64	1	3	9	8	3	III	45	III	44	20	P	13	17
10.12	1	4	9	8	4	IV	42	III	42	20	P	13	17
11.01*	1	5	9	8	5	IV	45	III	43	21	P	13	17

* Juveniles.

cated near the distal end of the pelvic bone, projects posteroventrally through the integument of the ventral midline.

Scales were evident along the nape and anterior lateral line at approximately 11 mm SL on *P. paru* and 14 mm SL on *P. burti* and *P.*

triacanthus. In conjunction with a full complement of rays in all fins, the appearance of scales marked the beginning of juvenile stage.

Osteological development.—The cranial cartilages (e.g., orbital and otic cartilages, epiphysial tec-

trum) and parasphenoid-basioccipital bridge were evident on the smallest specimens of each species cleared and stained (Table 3). Initial ossification of the parasphenoid and the basioccipital had begun on specimens of each species by 5 mm SL. Most of the other neurocranial elements (e.g., frontal, parietal and supraoccipital) had begun to ossify by 7 mm SL on *P. paru* and 8 mm SL on *P. burti* and *P. triacanthus*.

Chondrification of the maxillary and dentary was evident on the smallest specimens of each species (Table 3). Chondrification of the premaxillary, operculum, and preoperculum had begun on 3.2 mm SL *P. paru* and by 3.6 mm SL on *P. burti* and *P. triacanthus*. Upper jaw development (i.e., premaxillary and maxillary) was similar to that described by Berry (1964) for advanced teleosts. The maxillaries formed prior to the premaxillaries but the premaxillaries grew posteriad to essentially exclude the maxillaries from the gape as larvae developed. Minute teeth were present on the pharyngeal sac, dentary and premaxillary of specimens approximately 4.7 mm SL of all three species. Teeth were added as these structures developed.

By about 5–6 mm SL, 5–7 spines were present along the preopercular margin on each species. These spines persisted throughout the size range examined although on some specimens 1 or 2 were reduced or absent.

Branchiostegal rays had begun to ossify by approximately 4 mm SL on all three species and included four supported by the ceratohyal and two by the epihyal.

During late preflexion or early flexion, anterior vertebrae usually began to form with neural and haemal spines developing before their respective centra. Centra began to ossify at the base of the neural and haemal arches with ossification progressively encircling the notochord. Vertebral development proceeded posteriad; however, the urostyle ossified prior to the preceding 3–4 vertebrae. All vertebrae were ossifying at approximately 7 mm SL on each species. Caudal vertebra counts overlapped among the three species. *P. paru* consistently had 17 caudal vertebrae, whereas *P. burti* and *P. triacanthus* had 17–18 and 18–19, respectively. However, on specimens greater than 7 mm SL, 86% (N = 22) of *P. burti* had 17 caudal vertebrae and 79% (N = 19) of *P. triacanthus* had 19.

Chondrification of the dorsal and anal pterygiophores began antieriad and continued pos-

teriad; ossification followed a similar sequence. All dorsal and anal pterygiophores were weakly ossified by 12 mm SL on all three species. Anterior to the dorsal pterygiophores were three predorsal bones which interdigitated with the neural spines on a one-to-one basis; a predorsal preceded the first, second, and third neural spines. Predorsal ossification occurred first on *P. paru* (6.7 mm SL) followed by *P. burti* (7.1 mm SL) and then *P. triacanthus* (8.4 mm SL).

On all three species, the cleithrum formed and ossified first (3.2–3.6 mm SL) followed by the supracleithrum (4.2–4.7 mm SL) then the postcleithrum (5.2–5.4 mm SL). Ossification of the coracoscaphular process coincided with initial development of rays in the pectoral fins and occurred at 5.2 mm SL on *P. paru* and 6.5–6.6 mm SL on both *P. burti* and *P. triacanthus*. The radials, the last elements of the pectoral girdle to ossify, initially ossified on 6.7 mm SL *P. paru*, 6.5 mm SL *P. burti*, and 8.4 mm SL *P. triacanthus*. Ossification of the basipterygium and pelvic spine occurred first on *P. paru* (6.7 mm SL), followed by *P. burti* (7.1 mm SL) and *P. triacanthus* (8.4 mm SL).

The three species of *Peprilus* exhibited identical caudal morphology. The caudal complex consisted of the following parts: 3 centra (2 preural and 1 urostyle); 1 neural spine; 1 specialized neural arch; 2 epurals; 1 uroneural fused to urostyle; 4 hypurals (2 + 3 and 4 + 5 fused); and 2 autogenous haemal spines. The hypurals supported the 17 principal caudal rays (9 upper + 8 lower), whereas the procurent rays were supported dorsally by the neural spine and epural bones and ventrally by the haemal spines. A procurent spur (Johnson 1975) was present.

Development of the caudal complex was first evident as a ventral thickening near the tip of the unflexed notochord. Hypurals 1–5 and the preural neural and haemal spines began to differentiate and chondrify on 4.2 mm SL *P. paru* and 4.6–4.7 mm SL *P. triacanthus* and *P. burti* with hypurals 2 + 3 slightly better developed than hypurals 1 or 4 + 5 on each species. The epurals were chondrified on 4.6–4.7 mm SL *P. burti* and *P. triacanthus* and on 5.2 mm SL *P. paru*, followed by chondrification of the neural arch on 5.2–5.4 mm SL specimens of each species. Hypural 6 began to form on 5.3 mm SL *P. burti* and on 6.6 mm SL *P. triacanthus* but was not evident on *P. paru* until initial ossification (6.7 mm SL). The uroneural was the last element to form on each species.

The urostyle and hypurals 2–5 began to ossify

first (by about 5.5 mm SL on all three species). Initial ossification of hypural 1 and the preural neural and haemal spines was evident by about 7 mm SL on each species. Hypural 6 and the uroneural were ossified on 7.1 mm SL *P. burti* and 8.4 mm SL *P. triacanthus* but on *P. paru*, hypural 6 ossified (6.7 mm SL) before the uro-neural (7.7 mm SL). The neural arch began to ossify earlier on *P. burti* and *P. paru* (about 6.6 mm SL) than on *P. triacanthus* (8.4 mm SL). The last elements to ossify were the epural bones; ossification was evident on 7.7 mm SL *P. paru*, 8.4 mm SL *P. burti*, and on 9.4 mm SL *P. triacanthus*. Ossification became more complete as larvae developed, but caudal elements remained chondrified distally throughout the size range examined.

DISCUSSION

Pigmentation and/or body depth differences distinguish *P. paru* from both *P. burti* and *P. triacanthus* at all sizes. On specimens less than about 5.5 mm SL, melanophores formed diagnostic lateral bands, one above and one below the midline on *P. paru*, whereas *P. burti* and *P. triacanthus* usually had only one or two lateral melanophores. Between 5.5–9 mm SL, *P. paru* were heavily pigmented laterally with melanophores distributed over most of the trunk except for the posterior one-quarter. In contrast, *P. burti* and *P. triacanthus* of the same size range were much less heavily pigmented with melanophores concentrated mainly along the nape and over the visceral mass. Body depth at pectoral separated *P. paru* from both *P. burti* and *P. triacanthus* greater than 9 mm SL. Body depth at the pectoral was greater than 60% SL (more than 65% SL on specimens greater than 13 mm SL) on *P. paru* but less than 58% SL on *P. burti* and *P. triacanthus* (Table 1). On specimens 10 mm SL and greater, the same proportional measurements also applied to body depth at anus (Table 1).

P. burti and *P. triacanthus* less than 4 mm SL can usually be separated by the number of ventral midline melanophores. Most *P. burti* had 4–8 melanophores between the hindgut and notochord tip, whereas most *P. triacanthus* had 11–17. The number of caudal vertebrae usually distinguished *P. burti* and *P. triacanthus* greater than 7 mm SL; most *P. burti* had 17 caudal vertebrae, whereas most *P. triacanthus* had 19. Specimens between 4–7 mm SL were not consistently distinguishable although *P. triacanthus*

often was more densely pigmented than *P. burti* along the ventral midline between the hindgut and posterior base of the hypurals. In addition, pigment usually appeared over the forebrain by 5–6 mm SL on *P. triacanthus* but not until 7–8 mm SL on *P. burti*.

Results of this study essentially agreed with observations on *P. paru* by Pearson (1941) and with existing information on *P. triacanthus* identification summarized by Martin and Drewry (1978). However, Pearson (1941) noted "what appears to be a secondary or true vent developed anterior to the gut" on *P. paru* less than 3.5 mm total length. Our observations indicate that this "secondary vent" (also found on *P. burti* and *P. triacanthus*) is only a mass of tissue ventrad to the hindgut and gradually disappears by 4 mm SL.

Developmental data provided by D'Vincent et al. (1980) on the Pacific pompano, *Peprilus simillimus*, indicate that this fish is less developed in terms of flexion, ossification, and transformation at comparable standard lengths than the species of *Peprilus* in the western North Atlantic.

In conclusion, developmental morphology does little to augment our understanding of the relationship between *P. burti* and *P. triacanthus*. Aside from rather subtle differences in pigmentation on earlier larvae and modally different vertebral counts on older individuals, *P. triacanthus* and *P. burti* are extremely similar. Nevertheless, on the basis of the above mentioned differences, most specimens can be assigned to recognizable types.

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